INITIAL FEEDING BY ANTARCTIC FISH LARVAE DURING WINTER AT SOUTH GEORGIA

by

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ABSTRACT. - Initial feeding is described for larvae of four fish species from a fjord at the sub-Antarctic island of South Georgia during winter (May to August 1980). The data are limited because few fish larvae were caught in winter by the shorebased sampling methods available. *Pagothenia hansoni* (11-30 mm standard length), fed on calanoid copepods including adult *Drepanopus forcipatus*. *Harpagifer georgianus* (6.5-11 mm SL) and *Parachaenichthys georgianus* (11-17 mm SL) fed on a range of copepod taxa and stages. *Pseudochaenichthys georgianus* (14-17 mm SL) was exclusively piscivorous. Species which begin feeding during winter are larger by summer than species which hatch later in the year and therefore have a larger trophic scope during the summer peak of zooplankton biomass and abundance. There is an annual succession of larval fish species in the plankton which spreads predation on copepods throughout the year, thereby increasing the stability of the food-web, and the number of species of fish larvae that the copepods can support. The timing of the early life history of the fish larvae in relation to that of their prey species may affect the amount of food available to them.

RÉSUMÉ. - La première alimentation des larves au cours de l'hiver (Mai à Août 1980) est décrite chez quatre espèces de poissons de l'île subantarctique de Géorgie du Sud. *Pagothenia hansoni* (11-30 mm de longueur standard) se nourrit de copépodes calanoides notamment d'adultes de *Drepanopus forcipatus*. *Harpagifer georgianus* (6.5-11 mm SL) et *Parachaenichthys georgianus* (11-17 mm SL) consomment plusieurs espèces et stades de copépodes. *Pseudochaenichthys georgianus* (14-17 mm SL) est exclusivement piscivore. Les espèces qui commencent à s'alimenter en hiver sont, en été, plus grosses que celles dont l'éclosion est plus tardive, et ont alors un spectre trophique plus large pendant le pic estival de zooplancton. Une succession des espèces de poissons au stade larvaire s'effectue ainsi au cours de l'année, répartissant dans le temps la prédation sur les copépodes, et accroissant la stabilité du réseau trophique et le nombre d'espèces de larves de poissons que les copépodes peuvent entretenir.

Key-words : Notothenioidei, *Pagothenia hansoni, Harpagifer georgianus, Parachaenichthys georgianus, Pseudochaenichthys georgianus*, PSW, South Georgia, Larvae, Feeding.

North and White (1987) have suggested that the reproductive strategies of Antarctic fish may be linked with the highly seasonal secondary production cycle. The larvae of *Notothenia angustifrons* and *Notothenia rossii* hatch and commence feeding for the first time in spring and summer when there are increased levels of food available, mainly the early copepodite stages of copepods. Other species such as *Chaenocephalus aceratus, Pseudochaenichthys georgianus* and *Parachaenichthys georgianus* have a different strategy, their larvae hatch in autumn and winter and begin feeding during this period. North and White (1987) speculated that during winter the larvae may feed on the overwintering stages of the smaller neritic species of copepods such as *Drepanopus forcipatus*. The diet of the larvae of four fish species, each from a different family of the Notothenioidei, has been examined from samples obtained during the winter.

MATERIALS AND METHODS

Larval fish were sampled at Cumberland East Bay, South Georgia (54°17' S, 36° 30' W) during the austral winter of 1980 (May to August), from the British Antarctic Survey's shore research station 'Grytviken' at King Edward Point. Specimens were sampled in the early evening (after dusk) by using various techniques including : dip net, 1m^2 neuston net towed at

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the surface, and SCUBA diving with a hand net. Samples were also collected during the day by SCUBA. The specimens were kept at ambient temperatures (+2 to -1.4°C) in seawater for up to two hours after capture then preserved in 10 % formalin solution (with equal parts of fresh and seawater, buffered with excess chalk and adjusted to pH 9 with borax).

The families, species and number of specimens in the present study were : Nototheniidae *Pagothenia hansoni* (29), Harpagiferidae *Harpagifer georgianus georgianus* (20), Bathydraconidae *Parachaenichthys georgianus* (15), and Channichthyidae *Pseudochaenichthys georgianus* (5), (nomenclature follows Fischer and Hureau, 1985). The low number of specimens examined was because few fish larvae could be caught in winter by the available sampling methods.

Fish were identified and measured at x 6-60 magnification using a binocular microscope (Wild M5) and a high power light source.

Measurements of fish standard length (SL) were made according to the recommendations of Hureau (1982). Fish eye diameter, in the anterio-posterior plane, and gape width, the internal width of the mouth, were measured using an eyepiece graticule and reflected light.

To examine the prey ingested by the fish the entire gut was first dissected free of the body and then the wall of the gut was carefully removed from prey items using fine needles. The stomach fullness of the larval fish was estimated on a linear scale of 0-4, 0 = empty, 1 = 1/4 full... 4 = full. Stomachs less than an eighth full were classified as empty. The amount of yolk-sac in the fish larvae was estimated as a proportion of the total volume of the abdomen.

Prey items were identified and measured using an eyepiece graticule with transmitted light. For copepods, measurements of width were prosome width, and length, prosome plus urosome length excluding furca. All measurements of fish and prey were in mm.

The correlation of variables was investigated by least squares linear regression using the MINITAB (c) statistical package and tested with Student's t-test. The 5 % level ($p < 0.05$) was considered significant.

RESULTS

Diet

The diet of the larval fish is summarized in Table I. The dominant prey items were unidentified copepodite stages of copepods and crustacean remains (mainly copepods). Of the identified copepod component *Drepanopus forcipatus* was a major item in the diet of *Pagothenia hansoni* (11-30 mm SL) and *Parachaenichthys georgianus* (11-17 mm SL). *Harpagifer georgianus* (6.5-11 mm SL) also fed mainly on copepods, its prey items also included a single immature amphipod and a small proportion of diatoms. *Pseudochaenichthys georgianus* (14-17 mm SL) preyed exclusively on fish larvae and this was supported by further unpublished observations during spring.

Prey number and gut fullness

The total number of prey items recovered from the gut of each fish species is given in Fig. 1 (except for *Pseudochaenichthys georgianus* where only five individuals could be examined). The majority of the three species that consumed copepods had consumed few prey items and this is reflected by the degree of gut fullness, most were a quarter to a half full (Fig. 2). Because the *Pagothenia hansoni* larvae were generally larger they often contained more prey items than the other copepod-eating species, although their guts were mostly a quarter or less full. Four of the five *Ps. georgianus* had consumed a single prey item the other was empty ; two had guts three-quarters full and two were half full. In all four species few fish had full guts.

Yolk-sac dimensions and prey number

All species examined had commenced feeding before all the yolk was absorbed. An

Table I : Prey in the diet of four species of larval fish during winter at South Georgia. A = *Pagothenia hansoni* ; B : *Harpagifer georgianus* ; C : *Parachaenichthys georgianus* ; D : *Pseudochaenichthys georgianus*.

Prey species, stage and sex		Predator and number of each prey			
		A (N=29)	B (N=20)	C (N=15)	D (N=5)
Diatoms			>3		
Crustacea:					
Copepoda		3			
Calanoides acutus	CII-III			1	
Clausocalanus laticeps			1		
Ctenocalanus sp.	CV	5			
Drepanopus forcipatus	CVI F	11	1	7	
	CVI M	5		3	
	CV	1		1	
	CIV	1			
	Unstaged			2	
Metridia lucens	CVI F			1	
	CV			1	
Metridia sp. copepodites		3	1		
Copepodite		32	36	7	
Nauplius		1	1		
Cyclopoid		1			
Oithona sp.		2	1	2	
Harpacticoid		2	4	1	
Crustacean remains - mainly copepods		37	4	2	
Amphipoda			1		
Fish:					
Nototheniidae					1
Pagothenia hansoni					2
Parachaenichthys georgianus					1

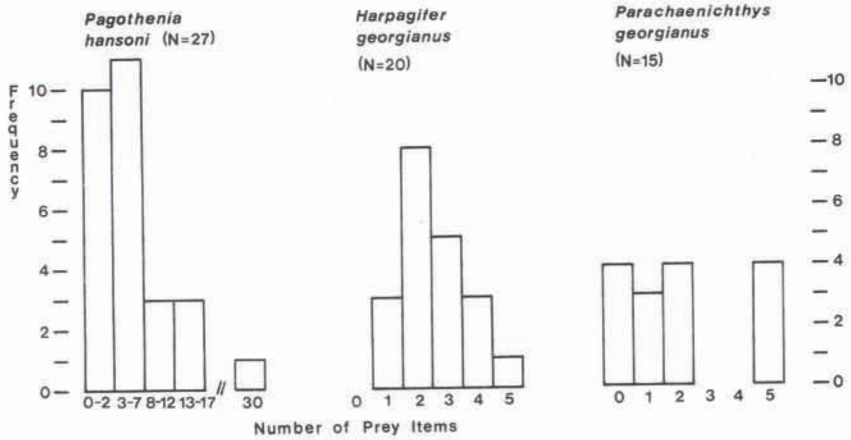

Fig. 1 : Frequency of the number of prey items in the diet of four species of larval fish during winter at South Georgia. Note two *P. hansoni* with low but uncertain number of prey items excluded.

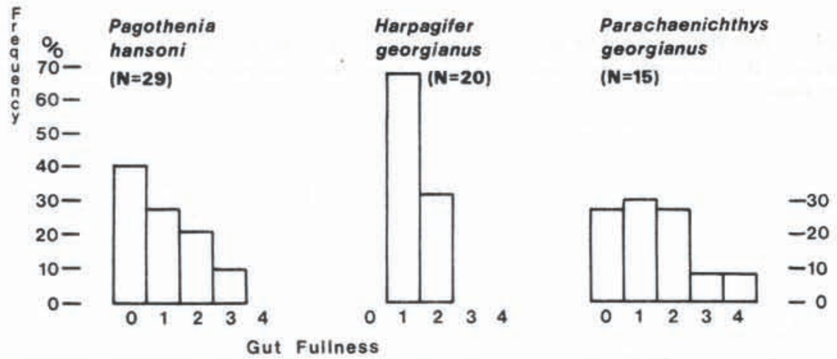

Fig. 2 : Percent frequency of gut fullness of four species of larval fish during winter at South Georgia.

individual *P. hansoni* in which the yolk-sac occupied most of the volume of the abdomen contained three prey items. Two specimens of *Pa. georgianus* with a large yolk-sac (>3/4 the volume of the abdomen) contained no prey items, whereas nine individuals with a small yolk-sac (<1/4 the volume of the abdomen) contained up to five prey. Most *H. georgianus* (6-9 mm SL) had little or no yolk but three specimens (7-9 mm SL) with a small amount of yolk contained two or more prey items. One specimen of *Ps. georgianus* which contained a trace of yolk had consumed a fish larva.

Fish size and eye diameter

There was a direct relationship between eye diameter (ED mm) and body length (SL mm) in the species *P. hansoni*, *H. georgianus* and *Pa. georgianus*:

P. hansoni	$ED = 0.10 + 0.062\,SL$,	$R^2 = 0.95$ $N = 27$
H. georgianus	$ED = 0.27 + 0.092\,SL$,	$R^2 = 0.60$ $N = 20$
Pa. georgianus	$ED = 0.46 + 0.043\,SL$,	$R^2 = 0.56$ $N = 14$

These relationships were used to calculate the length of partially digested fish in the diet of *Ps. georgianus*.

Prey size

The dimensions of the prey taken by the larvae are summarized in Table II a-b. The size of prey taken by the three copepod-eating species was similar. The length and width of prey taken by *P. hansoni* and *H. georgianus* had almost the same mean and range, but prey taken by *Pa. georgianus* were on average slightly longer and one third wider, although this difference is not statistically significant. In relation to body length the piscivorous *Ps. georgianus* consumed the largest prey and *H. georgianus* consumed the largest copepod prey (Table II c).

Prey size in relation to fish gape

Hunter (1981) reviewed the feeding ecology of marine fish larvae and recognised firstly, that fish gape width was generally proportional to fish length and was the limiting dimension in determining the size of prey a fish could ingest whole. Secondly, that width rather than overall length of an organism was the critical dimension in determining its potential as fish prey. Accordingly we have examined the relationships between these dimensions.

For all species, except *Ps. georgianus* (where the sample size was small), there was a positive correlation ($p<0.05$) between gape width and standard length (SL) (Table III). For *Pa. georgianus* however, the regression accounts for less than half the variability of gape width and this is thought to be due to the difficulty in measuring preserved specimens slightly damaged by capture. In *P. hansoni* maximum prey width increased with fish gape width indicating that

Table II : Summary of prey size by width and length, and prey to predator length ratio, for four species of larval fish during winter at South Georgia.

a. Prey Width (mm)

Species	mean	median	SD	min	max	N
Pagothenia hansoni	0.30	0.32	0.12	0.06	0.60	105
Harpagifer georgianus	0.30	0.30	0.12	0.08	0.54	29
Parachaenichthys georgianus	0.40	0.40	0.13	0.20	0.78	30
Pseudochaenichthys georgianus				0.76	1.07	2

b. Prey Length (mm)

Species	mean	median	SD	min	max	N
P. hansoni	0.79	0.76	0.30	0.20	1.50	35
H. georgianus	0.74	0.75	0.28	0.28	1.24	14
Pa. georgianus	0.92	0.95	0.28	0.38	1.62	20
Ps. georgianus	11.4		3.9	7.0	12.5	3

c. Prey/Predator Length Ratio

Species	mean	median	SD	min	max	N
P. hansoni	0.038	0.037	0.014	0.012	0.075	35
H. georgianus	0.092	0.096	0.038	0.036	0.185	14
Pa. georgianus	0.057	0.058	0.018	0.024	0.108	20
Ps. georgianus	0.77		0.24	0.50	0.94	3

Table III : The relationship between gape width on standard length for four species of larval fish during winter at South Georgia (all measurements in mm ; ns = slope not significantly different from zero).

Species	intercept	slope	R^2	N	P
P. hansoni	0.005	0.061	0.91	29	<0.05
H. georgianus	-0.309	0.104	0.81	18	<0.05
Pa. georgianus	-0.500	0.085	0.43	15	<0.05
Ps. georgianus	-0.865	0.109	0.26	5	ns

the size range of prey consumed increased with size of predator (Fig. 3). With a doubling of gape width, maximum prey size doubled in *P. hansoni* but only increased by a factor of 1.5 in *H. georgianus* although in both species a wide size range of prey was taken. No apparent increase in prey size with fish size was observed for *Pa. georgianus* of *Ps. georgianus*. The average width of prey consumed by *H. georgianus* was about half their gape width whereas that or *P. hansoni* was about one fifth of gape width. The width of prey consumed by *Pa. georgianus* varied from about one quarter to four fifths of gape width.

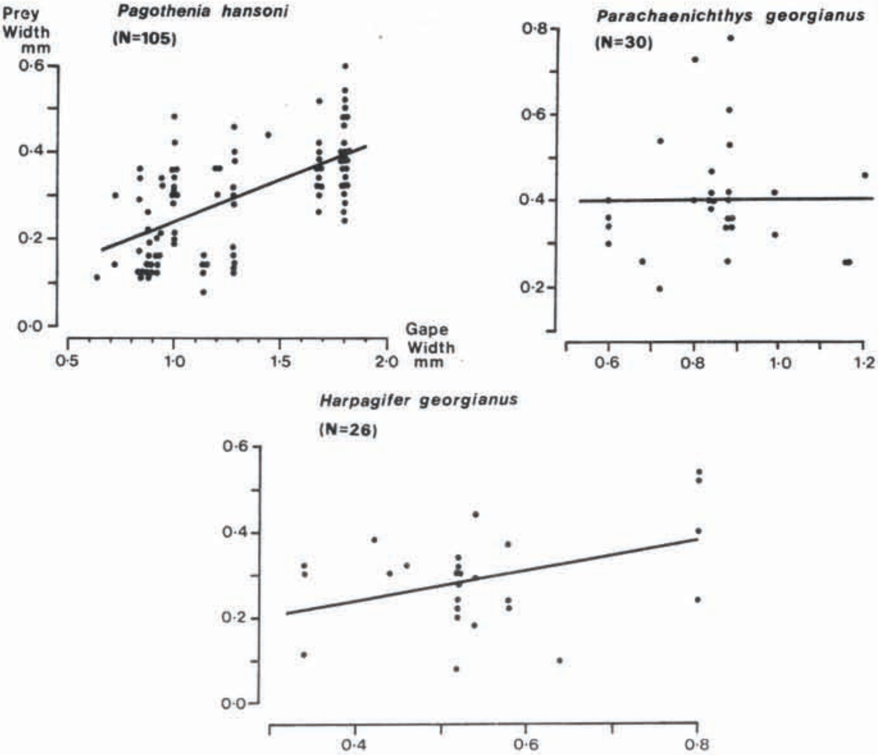

Fig. 3 : Prey width (PW) on gape width (GW) for three species of larval fish during winter at South Georgia showing individual data values and the predicted regression line : *P. hansoni* PW = 0.034 + 0.197. GW, $R^2 = 0.41$, $p<0.05$; *Pa. georgianus* PW = 0.400 + 0.004. GW, $R^2 = 0.0$, not significant ; *H. georgianus* PW = 0.116 + 0.320. GW, $R^2 = 0.10$, not significant.

DISCUSSION

Little is known about the early diet of Antarctic fish. Studies on larval *Pleuragramma antarcticum* in the Weddell Sea by Hubold (1985) have shown that the small pelagic pteropod *Limacina* sp. was an important dietary item in the high Antarctic. At the Antarctic Peninsula Kellermann(1986) found that larval *Nototheniops larseni* and *Pleuragramma antarcticum* preyed upon calanoid copepod eggs and nauplii, cyclopoid copepods and tintinnids. The results of this study, from limited data, on larvae from South Georgia and North and Ward (in press) are the first to report on the diet of species which hatch and begin feeding in winter.

In this study the overwintering stages of copepods were shown to be the major component in the diet of the early larvae of three fish species *(P. hansoni, Pa. georgianus,* and *H. georgianus).* The same has also been found for early larvae of *Champsocephalus gunnari* and *Chaenocephalus aceratus* and later larvae of *Nototheniops nudifrons* for which adult female *Drepanopus forcipatus* were most important in their diet during late winter/early spring at South Georgia (North and Ward, in press). Ward (1989) has shown that small species of copepods, in particular *D. forcipatus,* dominate the zooplankton by both number and biomass in the nearshore fjord ecosystem at South Georgia. Therefore, the larval fish were utilising the greatest prey resource available to them. Species diversity in the diet of larval fish was generally low and probably reflects the upper size range of zooplankton which the larvae are capable of consuming that was present in the water column.

Winter feeding success appeared to be low with most fish having guts less than half full, however, most fish larvae are reported to feed mainly during daylight (Hunter 1981) and because most of our specimens were caught in the early evening it is likely that some digestion of prey had occurred. There were low numbers of prey items in larvae with moderately sized yolk sacs. Experimental evidence cited by Hunter (1981) suggests that feeding success in a number of species is generally poor at the commencement of feeding. In this study the low number of prey items in larvae with moderate sized yolk-sacs may indicate that this is also a feature of Antarctic fish larvae. However, low prey numbers may also reflect low feeding activity and small gut size. Feeding did, however, start before all the yolk was absorbed in all the species investigated.

The Antarctic marine environment is highly seasonal with a strong pulse of production occurring over the summer period and a minimum in winter (Clarke, 1988). The timing of spawning and subsequent hatching of larvae in relation to this annual cycle will largely determine the amount of food available to them. Several species lay large yolky eggs which hatch during autumn and winter. These larvae appear to survive by feeding on the overwintering stages of neritic copepods and thus their life cycles are not directly linked to the peak of secondary production in late spring. Larvae which hatch in winter are larger by spring and therefore have a larger trophic scope during the period of elevated production. During summer, winter hatching species, eg. *Chaenocephalus aceratus* (North, unpub.), are able to prey upon larval fish which hatch in spring and summer (North and Ward, in press) in addition to feeding on other zooplankton. Therefore hatching early in the season seems to be advantageous to species which are piscivorous as larvae.

North and White (1987) showed that there was a succession of species hatching throughout winter to summer at South Georgia. The order of hatching was familial ; a bathydraconid then channichthyids, followed by the nototheniids. The initial feeding period of these larvae are likely to be broadly synchronised with the life cycles of their food species. Temporal partitioning of this kind will spread predation more evenly throughout the year thus increasing the stability of this part of the food web. This suggests that food for early larvae may be limiting the amount of larvae which can coexist in the ecosystem at any given time of year. These findings are in agreement with Clarke (1988) who postulated that production (growth and reproduction) of polar marine ectotherms is limited not by temperature but by food availability and that the seasonality of their growth is linked to their position in the food web. Thus the seasonality of production is likely to be more extreme in obligate herbivores such as small copepods than the fish which prey upon them.

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